First glimpse into Lower Jurassic deep-sea biodiversity: \emph{in situ} diversification and resilience against extinction

Ben Thuy\textsuperscript{1}, Steffen Kiel\textsuperscript{2}, Alfréd Dulai\textsuperscript{3}, Andy S. Gale\textsuperscript{4}, Andreas Kroh\textsuperscript{5}, Alan R. Lord\textsuperscript{6}, Lea D. Numberger-Thuy\textsuperscript{1}, Sabine Stoehr\textsuperscript{7} and Max Wisshak\textsuperscript{8}

\textsuperscript{1}Natural History Museum Luxembourg, Department of Palaeontology, 24, rue Münster, Luxembourg 2160, Luxembourg
\textsuperscript{2}Geoscience Centre, Geobiology Group, University of Göttingen, Goldschmidtstrasse 3, Göttingen 37077, Germany
\textsuperscript{3}Hungarian Natural History Museum, Department of Palaeontology and Geology, 1431 Budapest, Pf. 137, Hungary
\textsuperscript{4}School of Earth and Environmental Sciences, University of Portsmouth, Burnaby Building, Burnaby Road, Portsmouth PO1 3QL, UK
\textsuperscript{5}Natural History Museum Vienna, Department of Geology and Palaeontology, Burgring 7, Vienna 1010, Austria
\textsuperscript{6}Senckenberg Research Institute, Micropalaeontology I, Senckenberganlage 25, Frankfurt 60325, Germany
\textsuperscript{7}Swedish Museum of Natural History, PO Box 50007, Stockholm 10405, Sweden
\textsuperscript{8}Senckenberg am Meer, Marine Research Department, Südstrand 40, Wilhelmshaven 26382, Germany

Owing to the assumed lack of deep-sea macrofossils older than the Late Cretaceous, very little is known about the geological history of deep-sea communities, and most inference-based hypotheses argue for repeated recolonizations of the deep sea from shelf habitats following major palaeoceanographic perturbations. We present a fossil deep-sea assemblage of echinoderms, gastropods, brachiopods and ostracods, from the Early Jurassic of the Glasenbach Gorge, Austria, which includes the oldest known representatives of a number of extant deep-sea groups, and thus implies that \emph{in situ} diversification, in contrast to immigration from shelf habitats, played a much greater role in shaping modern deep-sea biodiversity than previously thought. A comparison with coeval shelf assemblages reveals that, at least in some of the analysed groups, significantly more extant families/superfamilies have endured in the deep sea since the Early Jurassic than in the shelf seas, which suggests that deep-sea biota are more resilient against extinction than shallow-water ones. In addition, a number of extant deep-sea families/superfamilies found in the Glasenbach assemblage lack post-Jurassic shelf occurrences, implying that if there was a complete extinction of the deep-sea fauna followed by replacement from the shelf, it must have happened before the Late Jurassic.

1. Introduction

Thanks to intense research efforts during the last few decades, it is now generally acknowledged that the deep sea supports one of the highest levels of biodiversity on Earth, while differing fundamentally from shallow marine and terrestrial ecosystems [1,2]. Yet, the evolutionary processes that have shaped the unique attributes of the deep sea are still controversial. Growing evidence that the deep sea was anything but stable and unchanging through time has challenged the initial concept of the deep sea as a refuge for ancient lineages excluded from shelf habitats. Debates have focused on the impact of variations in temperature, oxygenation and circulation mode on the colonization of deep habitats, and at least for the late Cenozoic, deep-sea sediment cores have provided extensive benthic foraminifer and ostracod microfossil evidence in this respect [3,4]. Biogeographic patterns and molecular clock estimates have yielded dates which predominantly converge to a latest Mesozoic or early Cenozoic origin of the modern deep-sea fauna [5–9]. Testing these hypotheses and exploring older deep-sea biodiversity using direct fossil evidence, however, has been hampered so far by the sparse record of
deep-sea faunas older than the Late Cretaceous [6]. The recent
discovery of a modern-type echinoderm assemblage from
Lower Cretaceous bathyal deposits of the subtropical north
Atlantic [10] demonstrated that direct fossil evidence of deep-
sea biodiversity exists in sediments beyond Late Cretaceous
age and showed that the origin of at least some modern
deep-sea groups is to be sought in even older strata.

2. Geological context

We here present fossil remains of a newly discovered diverse
deep-marine assemblage retrieved from marls of the Kehlbach
and Scheck Members (informally known as ‘Hauptknollenbrek-
zie’) within the Adnet Formation, exposed in the Glasenbach
Gorge, south of Salzburg in the northern Calcareous Alps,
Austria. These sediments are interpreted as a giant slump deposit
derived from the slope of a submarine high in the former north-
ern Tethys Ocean, and their ammonite fauna indicates an Early
Jurassic age (from the late Sinemurian Echioceras raricostatum
Zone to the late Pliensbachian Anmatheus margaritatus Zone)
[11,12]. Palaeo-depth reconstructions suggest at least 1000 m
for the slump components, based on subsidence models of
the area, sedimentological comparisons with present-day
equivalents and the presence of very similar lithologies directly
overlying both oceanic and deeply submerged continental
crust in the Jurassic of the north Atlantic [11,13], as well as the
absence of light-dependent benthic organisms even on the sub-
marine tops of the source area of the slumping mass [12].
These estimates are supported by our palaeobathymetric analy-
sis using microbioerosion trace fossils in 15 bivalve and
brachiopod shell fragments and belemnite rostra. Not a single
unequivocal trace of a phototrophic chlorophyte or cyanobacter-
iun, which could indicate a photic environment, was found.
Rather, all identified traces are produced by heterotrophic organ-
isms (mostly marine fungi) and are typical constituents
of aphotic trace fossil assemblages (figure 1) [14]. Thus, the material
studied herein must have been deposited at a palaeo-depth
exceeding the lower limit of sunlight influence in the water
column, which, in the present case (low palaeo-latitude sea
with low water turbidity, deduced from the low sedimentation
rate [11]), was between 150 m (deepest regular phototrophic
records during settlement experiments [15]) and 370 m (deepest
known occurrence of phototrophic microendoliths [16]), and
thus well below regular palaeo-shelf depths.

Further evidence supporting a bathyal palaeo-depth is pro-
vided by the ostracod assemblage of the Glasenbach fauna,
which includes only forms lacking eyes or other signs of

Figure 1. Scanning electron microscope images of microboring trace fossils (in order of abundance) prepared as epoxy resin casts from mollusc shells from the
Sinemurian–Pliensbachian (Early Jurassic) of the Glasenbach section, Austria. (a) Semi-cylindrical resin cast of a belemnite rostrum exhibiting a large number of
microborings; (b) the dominant fungal microboring Polyactina araneola, in modern seas produced by the fungus Conchyliastrum; (c) the aphotic index ichnotaxon
Orthogonum lineare, producer unknown but most likely a fungus; (d) cluster of Flagrichnus profundus, produced by schizochytrid fungi; (e) Orthogonum giganteum,
producer unknown; (f) Saccomorpha isp., presumed fungal trace; (g) Podichnus centrifugalis, attachment scar of a juvenile brachiopod pedicle; (h) Platydendrina
convexa, producer unknown; (i) unknown dichotomously branching dendrinid microboring with affinity to the ichnogenus Abeliella. Scale bars equal 1 mm in (a),
10 μm in (b,d,f) and 100 μm in (c,e,g–i).
photoreception. In addition, it almost exclusively consists of members of the extant eurybathic Bairdioidea, and thus fundamentally differs from all known coeval ostracod assemblages from shelf depths [17,18] and instead resembles a coeval assemblage found in slope deposits from Turkey [19]. The Glasenbach assemblage thus provides a unique window into Early Jurassic deep-sea biodiversity and predates the late Mesozoic oceanic anoxic events commonly considered to have triggered extinction in the deep sea and subsequent replacement from the shelf.

3. Material and methods

Specimens were collected in the field or picked from washed residues. Figured specimens were deposited at the Natural History Museum in Vienna. Families and, where applicable, superfamilies were chosen as basis for the faunal analyses because they were found to represent a compromise between taxonomic resolution and comparability with modern communities. Identifications of dissociated echinoderm plates followed latest taxonomic recommendations [20–22].

To assess the origin, resilience and bathymetric range shifts of the deep-sea fauna, we classified the families/superfamilies of the Glasenbach assemblage as well as coeval shelf (less than 200 m palaeo-depth) faunas [20,21,23–36] as extinct, or extant and, according to their present-day bathymetric distribution, typically deep, typically shallow, or without depth preference (eurybathic) (figure 3; electronic supplementary material, table 1). Our bathymetric classification was based on the averaged mean depth distribution of the extant species of the families/superfamilies (calculated by averaging the upper and lower distribution boundaries for each species and by computing the arithmetic mean of the obtained values for each family/superfamily): typically deep—averaged mean depth greater than 500 m; typically shallow—averaged mean depth shallower than 200 m; eurybathic—averaged mean depth between 200 and 500 m. The upper boundary of the deep sea is commonly set between 200 and 500 m, in line with the fading of seasonal variations in physical parameters (e.g. temperature) and of the influence of sunlight [2,6,37–39]. We adopted a conservative approach using the 500 m boundary to minimize the impact of potential outliers from shelf depths. Microbioerosion trace fossils were analysed by applying the vacuum cast-embedding method and scanning electron microscopic imaging to visualize the delicate microborings in decalcified polymer-resin casts [14]. Statistic tests were performed using the software package PAST v. 2.13 [40].

4. Results and discussion

Among the several thousand available specimens, we distinguished at least 68 species belonging to four different phyla, i.e. echinoderms (ophiuroids, asteroids, echinoids and crinoids), molluscs (gastropods), brachiopods and crustaceans (ostracods) (figure 2 and electronic supplementary material).

This assemblage includes the extant, typically deep ophiomycetid ophiuroids, basal pterasterid asteroids and gwynioid brachiopods. These fossils predate the hitherto oldest record of these groups from Middle Jurassic shallow-water deposits by more than 25 Myr [20,21,23,24]. In addition, four extant deep-sea groups present in the Glasenbach assemblage, namely benthopectinid asteroids, eudesicrinid crinoids and...
dynamics, we compared the number of extant families/superfamilies in the Glasenbach assemblage and in coeval shelf faunas that retained their Early Jurassic depth preference until today versus those that did not. In the case of the Glasenbach assemblage these are the typically deep and eurybathic groups and in the case of the shelf fauna, the typically shallow and eurybathic groups. Among the echinoderms, significantly more deep-sea inhabitants retained their Early Jurassic depth preference to the present day than did coeval shelf inhabitants (Fisher’s exact test, $p = 0.0002$); among gastropods, these proportions are indistinguishable. Although more deep-sea brachiopods retained their Early Jurassic depth preference than those in shallow water, this difference is not statistically significant (Fisher’s exact test, $p = 0.1$), possibly because many extant brachiopods are most common at depths between 100 and 300 m [23] and are thus classified as eurybathic rather than typically deep according to the criteria applied here. Thus, depth-related turnover, reflecting how many extant groups have undergone shifts in their preferred depth distribution since the Early Jurassic, was higher at shallow depths than in the deep sea among echinoderms and probably in brachiopods, but not among gastropods. These results call for caution when using a single taxonomic group as a model to explore evolutionary patterns controlling deep-sea biodiversity.

The Glasenbach assemblage lacks extant shallow-water families/superfamilies, except for a single gastropod superfamily (Neritoidae). Thus, it seems that once families/superfamilies had colonized the deep sea, they either remained there or became extinct. This implies first that deep-sea environments provide higher evolutionary stability than shallow-water environments, and second that bathymetric shifts, in contrast to bathymetric extensions, from the deep sea to shallow waters are unlikely. Many extant deep-sea families/superfamilies present in the Glasenbach assemblage occur also in Early Jurassic shallow-water settings. Their restriction to the deep sea today results from a restriction of their once broad bathymetric range. This loss of shallow-water representatives among the once eurybathic groups seems to be a continuous process through geological time [43], as suggested by the last shelf occurrences of some of the Glasenbach families/superfamilies: e.g. Eudesicrinidae in the Late Jurassic [21], Zeillerioidea in the Early Cretaceous [23], and Pleurotomarioidae in the Cenozoic [44].

Several present-day deep-sea families, including Benthopectinidae, Aspidodiadematidae, Eudesicrinidae and Ophiomycetidae, lack a post-Jurassic fossil record at shelf depths but were already present in the Early Jurassic Glasenbach deep-sea assemblage. Had there been a complete extinction of the deep-sea fauna followed by recolonization from shelf seas since the Early Jurassic [1,5], it must have happened before the Late Jurassic. This further highlights the resilience of the deep sea against major palaeoceano-graphic perturbations and sheds further doubt on the global extent and/or devastating nature of the so-called anoxic events during the late Mesozoic [10,45–47].

5. Conclusion

In summary, our results imply that two macroevolutionary processes have concurrently contributed to deep-sea biodiversity since the Early Jurassic: the potential to generate higher-level taxonomic diversity and resilience against major palaeoceano-graphic perturbations. We show for the first time, to our
knowledge, that higher level taxa can originate in the deep sea, expand to shelf depths and survive in the deep sea even after having gone extinct in the shallow seas again. We speculate that the resilience of the deep sea results from the sheer size of the environment combined with the great dispersal potential of the deep-sea benthos, increasing the chance for taxa to survive in deep-sea refuges and to subsequently re-expand. The potential to generate diversity might result from the many unique attributes of the deep-sea environment [2], which require unique adaptations that can only evolve in situ. Whatever the causes, our results shed new light on the role of the deep sea as a macroevolutionary source and reservoir of biodiversity, as well as on its potential to contribute to shallow-water diversity.

The latter point in particular calls for a careful reappraisal of the impact of deep-sea trawling and mining activities on marine biodiversity.

Acknowledgements. We thank H. Hess for assistance with the identification of crinoid material, and G. Moosleitner for providing part of the fossil material.

Funding statement. Part of this study benefited from the support of EU-funded Synthesys grant nos. SE-TAF-2674 and SE-TAF-1297 to B.T., and GB-TAF-2781 to A.D. The study of brachiopods was supported also by the Hungarian Scientific Research Fund (OTKA K77451). Further financial support was provided by the Deutsche Forschungsgemeinschaft through grants Ki802/6-1 and Ki802/8-1 to S.K.

References

31. Gründel J. 2007 Jurassic Gastropoden aus der Betakalkbank (oberes Sinemurium, obere Obtusum-


